Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 5: The genera *Plumarella* Gray, 1870; *Acanthoprimnoa*, n. gen.; and *Candidella* Bayer, 1954

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Abstract.—The nine western Atlantic species belonging to three genera, *Plumarella, Acanthoprimnoa,* and *Candidella,* are described and illustrated. Four new species of *Plumarella* are described, as well as one new species of *Acanthoprimnoa*; the genus *Acanthoprimnoa* is also described as new, differentiated from *Plumarella* by lacking tubercles on the undersurfaces of its sclerites. Two western Pacific species are transferred to *Acanthoprimnoa*: A. serta and A. cristata. Three varieties are recognized of the common *Plumarella pourtalesii,* one previously described as a variety (*P. p. robusta*) and another proposed herein (*P. p. var. obtusa*). A dichotomous key and table of comparisons is provided for the species and forms of *Plumarella,* as are a table of comparisons for the two Atlantic species of *Acanthoprimnoa,* and an indented key to the eleven genera of western Atlantic Primnoidae. Specimens of these genera were found to be extremely common at lower shelf and upper slope depths primarily in the temperate western Atlantic; rover 1500 specimens were examined in this study, including types of all included species.

This is the fifth in a series of revisions (Cairns 2001; Cairns & Bayer 2002, 2003, 2004) of the western Atlantic deep-water octocorals, and the fourth dealing with the Primnoidae, a family consisting of about 205 species and 32 genera worldwide, of which approximately 33 species and 11 genera occur in the western Atlantic, Baver's revision of western Atlantic Calyptrophora (2001) should also be considered as the first unnumbered part of this series. which also deals with primnoids. In order to facilitate identification at the generic level within this family a key is provided below for those 11 genera that occur in the western Atlantic. Two genera occur twice in the key since they have both dichotomous and pinnate branching. In this part we review the genera Plumarella and Candidella, as well as describe a new genus, Acanthoprimnoa, separated from Plumarella on the basis of its lacking tubercles on

the undersurfaces of its sclerites. Specimens of *Plumarella* and *Acanthoprimnoa* are extremely common at shelf and upper slope depths (137–1160 m) in the western Atlantic, occurring there opportunistically as weeds do on dry land. Ironically, species of these two genera were previously known from only 11 stations and as many specimens from the western Atlantic; this report lists approximately 1425 specimens from 145 localities. The thrid genus, *Candidella*, is known from deeper water (514–2139 m), and occurs farther north (New England Seamounts) as well as in the eastern Atlantic.

Indented Key to the 11 Western Atlantic Genera of Prinnoidae (fraction indicates number of western Atlantic species/total number of species; genera in bold face treated in this part)

I. Colonies unbranched or extremely sparsely branched: Primnoella (4/14)

- II. Branching in the form of a bottlebrush: *Thouarella* (1+/25)
- III. Colonies pinnately branched
 - A. Polyps arranged in whorls: Callogorgia (3/28)
 - B. Polyps arranged biserially and alternately
 - Tubercles not present on undersurfaces of sclerites: Acanthoprimnoa (2/4)
 - Tubercles present on undersurfaces of sclerites
 - Undersurface of opercular scales with a prominent keel: Amphilaphis (1/6)
 - b. Undersurface of opercular scales without a longitudinal keel: *Plumarella* (6/ 20)
- IV. Colonies dichotomously branched
 - A. Polyps arranged in whorls
 - Polyps face outward from branch; 4 marginal scales: Candidella (1/4)
 - Polyps face up or down; 2 marginal scales
 - Polyps encased by only two pairs of large abaxial body wall scales
 - Members of two pairs of body wall scales inseparably fused to form a complete ring surrounding polyp; polyps face up or down: Calyptrophora (4/13)
 - Body wall scales not fused; polyps face downward: Paracalyptrophora (3/6)
 - Polyps encased by 3 or 4 pairs of large abaxial body wall scales: Narella (7/25)
 - B. Polyps arranged biserially and alternately
 - Tubercles not present on undersurfaces of sclerites: Acanthoprimnoa (2/4)
 - Tubercles present on undersurfaces of sclerites: *Plumarella* (6/20)

C. Polyps irregularly arranged: Primnoa (1/3)

Material and Methods

This study was based on the examination of approximately 1505 specimens, collected at 161 deep-water stations by 18 research vessels (Appendix: Station data). Except for those reported from the *Bibb* and *Atlantis*, which were borrowed from the MCZ, the specimens are deposited at the National Museum of Natural History (USNM). Synonymies for all species are purported to be complete for all previously published records. Unprefaced SEM stub numbers pertain to the series made by Bayer; those preftaced with C, to the series made by Cairns.

The following abbreviations are used: Alb—U.S.F.C.S. Albatross; Atl—R/V Atlantis; BM—British Museum (now The Natural History Museum, London); CI—R/ V Colombus Iselin; G—R/V Gerda; Gos— R/V Gosnold; H:W—height to maximum width of an opercular or marginal scale; JS—Johnson-Smithsonian Deep-Sea Expedition (Caroline); MCZ—Museum of Comparative Zoology, Harvard, Cambridge; O—M/V and R/V Oregon and Oregon II; P—R/V Pillsbury; SB—R/V Silver Bay; USNM—United States National Museum (now the National Museum of Natural History, Smithsonian, Washington, D.C.).

> Subclass Octocorallia Order Gorgonacea Suborder Calcaxonia Family Primnoidae Gray, 1858 Genus *Plumarella* Gray, 1870

- Cricogorgia Milne Edwards, 1857:6, pl. B2, fig. 6 (nom. nud.).—Gray, 1870:36–37.
- Plumarella Gray, 1870:36.—Studer, 1887; 51.—Wright & Studer, 1889;73–74, 281.—Versluys, 1906:13–14.—Kinoshita, 1908:6–8.—Kükenthal, 1915:144; 1919:340–342; 1924:255.—Deichmann, 1936:155–156.—Bayer, 1956:F220.— Fabricius & Alderslade, 2001:244–245.

Type species.—Gorgonia penna Lamarck, 1815, by subsequent designation (Kükenthal 1915:144).

Diagnosis.-Primnoidae with a well-defined operculum; polyps usually inclined apically, each polyp completely surrounded by 8 rows of body wall scales; polyps arranged biserially or irregularly, but never in whorls; 8 marginal scales, often pointed or spinose; undersurfaces of all sclerites tuberculate, opercular scales not keeled; colonies uniplanar, usually pinnately (plumose) branched but sometimes dichotomous.

Distribution.-Western Pacific; Patagonia; western Atlantic; 10-1914 m.

Remarks .- The only revision of the genus Plumarella was that of Kükenthal (1919), reiterated in 1924 (Kükenthal, 1924), which included the description and synonymy of all 17 species as well as a key to their identification. He used the following characters to distinguish species, as emphasized in his key: shape of distal edge of marginal scales, presence of a longitudinal keel on the body wall scales, number of scales in the ab- and adaxial body wall rows, polyp size, and texture of surface of body wall scales. These characters have also been used in this review (Table 1), along with the additional characters such as branching mode, terminal branchlet length and flexibility, number of polyps/cm branch length, shape of the operculars, presence of tubercles on the undersides of the sclerites, ornamentation on the edges of the opercular scales, and coarseness of coenenchymal granulation. the last three characters being used to distinguish a closely related new genus once confused with Plumarella.

Key to the Species and Forms of the Six Species of *Plumarella* known from the Western Atlantic

- Distal edges of marginal scales straight, gently rounded or only slightly angular
- 1'. Distal edges of marginal scales prominently spined
 7

2. Branching alternate pinnate; colonies
often large (up to 33 cm) 3
2'. Branching dichotomous; colonies fairly
small (less than 11 cm) P. dichotoma
3. Body wall scales smooth 4
3'. Body wall scales granular
4. Closely-pinnate branching; opercular
scales elongate and granular; 10-12
polyps/cm P. pellucida
4'. Loosely-pinnate branching; opercular
scales shorter and smooth; 14-21 pol-
vps/cmP. laxiramosa
5. Distal edges of marginal scales of some
polyps in a colony slightly angled (but
not spinose) P. pourtalesii var. obtusa
5'. Distal edges of marginal scales straight
to slightly rounded 6
6. 11-13 polyps/cm; distance between pol-
vps on one side of branch 1.0-1.2 mm
P pourtalesii var typical
6'. 14-16 polyps/cm; distance between pol-
vps 0 5–0 8 mm
P. pourtalesii var. robusta
7. Each marginal scale with a prominent
spine P. aurea
7' Only 4–7 marginal scales with an elon-
gate needle-shaped spine those scales
corresponding to operculars with at
least one uncovered edge P aculeata
ioust one uncovered edge
Blumanalla nountalogii (Vomill 1992)
Fundrena pouralesti (vertili, 1883)

Figs. 1A-B, 2A-C, 3A-C

- Primnoa Pourtalesii Verrill, 1883:28–29, pl. 2, figs. 2, 2a–e (S. Carolina).—Not Hargitt & Rogers, 1901:281, fig. D (probably A. goesi).
- Plumarella pourtalesi.—Wright & Studer, 1889:73, 74, 280 (new comb.).—Versluys, 1906:15–16 (comments only).
- Plumarella pourtalesii.—Versluys, 1906: 342 (key), 345–346 (German translation of Verrill); Kükenthal, 1919:345–346; 1924:257–258 (same as 1919).—Deichmann, 1936:156, pl. 25, figs. 17–18, pl. 26, figs. 10, 10a (two new records: Bibb 22, MCZ 4822 and Bibb 135, MCZ 4821).—Bayer, 1954a:281 (listed); 1956: F220, fig. 159-7; 1957:388 (two records, forma *obtusa*).—Bayer, Grasshoff & Verseveldt, 1983; fig. 53.—Bayer, 1973; fig.

	P. pourtalesti typical (Verrill, 1883)	P. pourtalesii var. robusta (Deichmann, 1936)	P. powralesil var. obtusa	P. pellucida, n. sp.	P. laxiramosa, n. sp.
Branching; Maximum col- ony height	Regular, alternate, close- pinnate; 33 cm	Regular, alternate, close- pinnate; 30 cm	Regular, alternate, close- pinnate; 19 cm	Regular, alternate, close- pinnate; 17 cm	Regular, alternate, loose- pinnate; 24 cm
Branch length and flexibil- ity	To 55 mm; flexible	To 50 mm; stiff	as in var. robusta	To 60 mm; stiff	To 80 mm; limp
Polyp height, diameter (mm); polyps/cm; orien- tation	0.9-1.2, 0.5-0.6; 11-13; inclined upward	1.1-1.2, 0.65; 14-16; in- clined upward	as in var. <i>robusta</i>	1.1, 0.65; 10-12; inclined upward	1.1-1.2, 0.65; 14-21; in- clined upward
Distal edge of marginals	Smooth, straight to rounded (scalloped)	as in typical var.	Triangular (obtuse angle)	Smooth, straight to rounded	Smooth, rounded
Scales per body wall row: abaxial/adaxial	5-6/4-5	as in typical var.	as in typical var.	6/5	6-7/5
H: W of operculars Scale ornamentation: oper-	1.5-1.9 Low apical ridges: granu-	as in typical var. as in typical var.	as in typical var. as in typical var	1.7-2.4 (curved) Granular no videose	1.8-1.9 Smooth on eldnoor
aculars; bw; coenenchy- mal	lar, granular (fine sand paper)		the model in on	smooth; granular (transhicent)	smooth; smooth
Tubercles present on un- derside of sclerites	Yes	Yes	Yes	Yes	Yes
Distribution	off N. Carolina to Cuba; 196-882 m	off N. Carolina through Straits of Florida; 183– 850 m	off Georgia through Straits of Florida; 183– 743 m	off N. Carolina through Straits of Florida; Ba- hamas; 549–1160 m	off N. and S. Carolina; 348-572 m
Branching; Maximum col- ony height	Dichotomous (lyrate); 11 cm	Dichotomous; 13 cm	Dichotomous, pinnate and lyrate; 12 cm	Dichotomous (4 cm) to pinnate (30 cm)	Loose pinnate (or lyrate) and dichotomous; 22
Branch length and flexibil- ity	To 40 mm; wiry to limp	To 100 mm; flexible	To 50 mm; stiff	To 40 mm; flexible	Long (to 55 mm); flaccid
Polyp height, diameter (mm); polyps/cm; orien- tation	1.1–1.3, 0.65; 8–10; per- pendicular on large branches	0.8-1.2, 0.8-0.9; 14-22; often perpendicular	1.4-1.8, 0.7-0.8; 10-12; perpendicular	0.8-1.2, 0.50; 13-15; in- clined slightly upward	Slender, 0.8-0.9, 0.4- 0.45, 11-13; slightly inclined
Distal edge of marginals	Smooth	Usually 8 prominent, marginal spines	Usually 5-6 (4-7) long, needle-shaped spines	7 tall, slender, bent spines	Straight or slight angle
Scales per body wall row: abaxial/adaxial	5-6/5-6	6-7/5-6	3-4/3-4	56/45	8-10

Table 1.—Table of comparisons of western Atlantic Plumarella and Acanthoprimnoa species and varieties.

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A. pectinata, n. sp.	1.6-2.2 e Ridged; granular; granu- lar	No	Off northeastern Yucatan Peninsula (164-476 m); Lesser Antilles, Straits of	FIORIDA (014-000 III)
A. goesi (Aurivillius, 1931)	1.8-3.9 Ridged; spinose; spinose	No	Straits of Florida to Yu- catan, Bahamas, Puerto Rico, Virgin Islands;	III CAC-/ CI
P. acuteata, n. sp.	1.6-2.2 All low granular (body wall sclerites may also be	Yes	Bahamas (northern Straits of Florida); 400–900 m	
P. aurea (Deichmann, 1936)	1.5–2.0 Smooth; smooth; smooth	Yes	off S. Carolina to Cuba; 310-878 m	
P. dichotoma, n. sp.	1.7–2.3 Granular; smooth; granu- lar	Yes	off S. Carolina to Florida: 494–1065 m	
	H : W of operculars Ornamentation of opercu- lars; bw; coenenchymal	Tubercles present on un-	Distribution	

Table 1.-Continued

16.—Bayer & Cairns (Verrill), 2004: pl. 26, fig. 1.

Plumarella pourtalesii var. robusta Deichmann, 1936:156–157, pl. 25, figs. 14–16, pl. 26, fig. 9.

Material examined.-Typical form: Alb-2416, 10 branches, USNM 10531; Alb-2662. 4 branches. USNM 14609: Alb-2663. 10 branches, USNM 14479; Alb-2667, 4 branches, USNM 49425; Alb-2668, 11 colonies, USNM 1019275; Alb-2669, over 50 colonies, USNM 14475; Atl-266-2, 6 colonies, USNM 1019276; Atl-266-7, 3 colonies, USNM 1021650; Atl-266-41, 7 colonies, USNM 1019277; Bibb 22, 2 branches, MCZ 4822 (reported by Deichmann 1936); Bibb 135, 2 branches, MCZ 4821 (reported by Deichmann 1936); Cape Hatteras SA6-5, 13 colonies, USNM 79782 (topotypic); CI-123, 9 colonies, USNM 1019278; CI-246, 26 branches, USNM 59491; Clelia 78, 1 colony, USNM 93910; Clelia 79A, 1 colony, USNM 93909; Combat 174, 1 colony, USNM 50799: Eastward 26017, 14 branches, USNM 59490; Eastward 26022, 2 branches, USNM 1019279; Eastward 26023, 10 branches (dry), USNM 1019280; Eastward 26028, 2 branches, USNM 1019281; Eastward 26052, 2 branches, USNM 1021652; G-170, 1 colony, USNM 1019305; G-177, 12 colonies, USNM 1019282; G-235, l branch, USNM 1019283; G-386, 3 colonies and SEM stub 250, USNM 53010; G-598, 1 colony, USNM 1019284; G-672, 1 colony, USNM 59498; G-785, 3 colonies, USNM 52994; Gos-2344, 10 branches, USNM 58448; Gos-2385, 10 colonies, USNM 56895; Gos-2387, 1 colony, USNM 57308; Gos-2413, 8 colonies, USNM 1019285; Gos-2414, 17 colonies, USNM 1019286; Gos-2461, 2 branches, USNM 1019287; O-1343, 3 branches, USNM 50183; O-1349, 3 branches, USNM 50443 (Baver 1958); O-11703, 2 colonies, USNM 59501; O-11717, 1 branch, USNM 59507; O-11725, 5 colonies, USNM 1019288; P-105, 2 branches, USNM 52999; SB-453, 2 branches, USNM



Fig. 1. A, Plumarella pourtalesii typical, Alb-2662; B, P. pourtalesii var. robusta, Alb-2416; C, P. aurea, station unknown; D, Acanthoprimnoa pectinata, Alb-2354. All scale bars = 1 cm.



Fig. 2. A-B, Plumarella pourtalesii typical: A, syntype, MCZ 5749, stereo oblique view of a polyp, B, G-386, stereo oblique view of a polyp. C, P. pourtalesii var. robusta. Combat 368, stereo view of operculum and surrounding marginals. D, P. pourtalesti var. obtusa. G-1314, stereo oblique view of a polyp. All scale bars = 0.25 mm.



Fig. 3. A-C, Plumarella pourtalesii typical (A-B, G-386; C, syntype, MCZ 5749): A, upper and undersurfaces of 5 opercular scales; B, upper surfaces of 3 body wall scales; C, upper and undersurfaces of 4 coenenchymal scales. D-E Plumarella pellucida (first opercular scale is from G-859, all other scales from the holotype): D, upper and undersurfaces of 5 opercular scales; E, upper and undersurfaces of 4 body wall scales; E upper and undersurfaces of 4 coenenchymal scales. All scale bars = 0.10 mm.

51260; syntypes (MCZ, USNM, see below).

Forma robusta: Alb-2416, over 25 colonies and 1 unnumbered SEM stub, USNM 49430, 49433; Alb-2666, 2 colonies, USNM 49422; Alb-2668, 10 branches, USNM 14474: Alb-2669, 8 branches, USNM 1019289; Anton Dohrn 6392, 3 colonies, USNM 1019290; Atl-266-4, 1 colony, 1 branch, USNM 1019291; Atl-266-40, 15 branches, USNM 1019293; Atl-266-41, 1 branch, USNM 1019292; Cape Hatteras SA6-1, 5 colonies, USNM 79783; CI-140, 1 branch, USNM 59497; Combat 368, 14 colonies and SEM stub 253, USNM 50800; Eastward 26023, 1 dry branch, 4 alcohol branches, USNM 1019294; G-170, 1 branch, USNM 1019295; G-177, over 20 colonies and 1 unnumbered SEM stub, USNM 52995; G-247, 1 colony, USNM 53012; G-261, 3 colonies, USNM 1019296; G-598, 7 colonies, USNM 52997; G-835, 3 branches, USNM 52998; Gos-2413, 5 branches, USNM 1019297; Gos-2461, 8 colonies, USNM 1019298; O-11726, 1 branch, USNM 73756; P-197, 1 colony, USNM 53013; holotype (see below).

Forma obtusa: Alb-2416, 1 branch, USNM 1019299; Alb-2668, 8 branches, USNM 1019300; Alvin 77-761, 2 colonies, USNM 1019301: Alvin 1335, 2 colonies, USNM 73741; Atl-3780, 10 dry branches, MCZ 54321; Cape Hatteras SA6, 8 branches. USNM 79781; CI-140. 3 branches. USNM 59495; CI-246, 9 branches, USNM 1019302; Eastward 26022, 1 branch, USNM 76986; Eastward 26023, 1 branch, USNM 1019303; G-56, 1 colony and 1 unnumbered SEM stub, USNM 53005; G-169, 7 colonies, USNM 53008; G-235, 8 colonies and SEM stub 260, USNM 53007; G-241, 9 colonies, USNM 53004; G-246, 2 branches, USNM 53003; G-261, 10 colonies, USNM 53009; G-386, 3 branches, USNM 1019304; G-391, 6 colonies and SEM 252, USNM 1019305; G-598, 1 colony, USNM 1019306; G-664, 3 branches, USNM 53001; G-679, 4 colonies, USNM 53002; G-1012, 1 colony, USNM 53011; G-1314, 9 colonies and SEM stub 251, USNM 53006; Gilliss, 25°50'N, 79°24'36'W, 603 m, 25 May 1973, 1 branch, USNM 79515; Gos-2387, 5 colonies, USNM 57306; O-1328, 1 colony, USNM 50528; P-209, 4 branches, USNM 53000.

Types and type localities.-Two colonies and several fragments of the typical form were mentioned by Verrill (1883) collected from Blake 318, all of which must be considered as syntypes. Deichmann (1936) attributed catalog number MCZ 4821 to the syntype series, but this number was preoccupied by Deichmann by specimens collected from "off Florida", thus the syntype series was later re-cataloged as MCZ 42887, and consists of three small branches. Four fragments and SEM stubs 249 and C1084 of one of these syntypes are also deposited at the USNM (5749). All syntypes are preserved in alcohol. Type Locality: Blake 318: 31°48'50"N, 77°51'50"W (Blake Plateau off South Carolina), 616 m.

The holotype of forma robusta, two small branches in alcohol, the largest 9 cm high, is deposited at the MCZ (4823). It also bears Verrill's personal number of 8032. It is also represented by an unnumbered SEM stub at the USNM. Type Locality: The type locality was stated to be "18 fms. off Alligator Reef, Florida" (Deichmann, 1936:157), but Deichmann correctly queried the extremely shallow depth of the collection. A newer label with this type indicates that it was collected at Bibb station 192 (24°48'05"N, 80°34'45"W: off Alligator Reef), at 216 m, this depth being more consistent with the known bathymetric range.

Diagnosis.—Distal edge of marginal scales rounded (scalloped) or straight; branching close pinnate, branchites of moderate length and stiff; body wall scales granular, surface of operculars ridged; 11– 13 polyps/cm (14–16 for forma *robusta* and obtusa).

Description.—Colonies are flabellate and pinnately branched (plumose), consisting of a main branch, which gives rise to 1-4 primary branches (depending on the size of the colony), each main and primary branch giving rise to numerous stiff branchlets up to 55 mm in length, in an alternating sequence (alternate pinnate). Although flabellate, colonies may be uniplanar or slightly convex, such that the polyps are directed toward the convex side. A branchlet occurs on the main branch within 5 mm of the base of the colony; additional branchlets occur at regular intervals of 1.8-3.2 mm on the main and primary branches, producing a characteristic zig-zag pattern for the larger branches, the branchlets being straight and parallel to one another. The main stem is usually anchored by a dense, white, calcareous holdfast, which is often attached to the dead corallum of a deep-sea scleractinian. The axis is vellow-brown or gold and longitudinally striate; overall the colony is white in alcohol. The largest colony (Combat 174) is 33 cm in height, 13 cm in width. and 2.7 mm in basal diameter, but most colonies examined were considerably smaller.

Polyps are arranged on all branches (i.e., main, primary, and branchlets) biserially in the plane of the flabellum in an alternating fashion, but angled upward such as to produce a 30°-45° angle with the branch, as well as being slightly curved toward the anterior (convex) side of the flabellum. Two to six polyps occur on the internodes of the main and primary branches. Polyps are rarely more than 1 mm in height, slightly wider at the apex (0.5-0.6 mm) than the base, and fairly well spaced: polyps on the same side of a branchlet are separated by 1.0-1.2 mm. In general, 11-13 polyps occur/cm of branchlet length, this number sometimes lower in small colonies.

Each polyp is encased by 8 opercular and 8 rows of body wall scales. The abaxial rows of body wall scales consist of 5 or 6 scales, the adaxial rows usually one less (4-5) scales), the latter rows always shorter due to having less scales and being located on the shorter, concave, side of the upturned polyp. The marginal scales are up to 0.37

mm in width, bearing sparse, low granules (10 µm in diameter) on their exterior surface and complex tubercles on undersurface (up to 13 µm in diameter). Body wall scales proximal to the marginals are progressively smaller. Body wall scales overlap one another within each row as well as overlapping the edges of the scales in both adjacent rows. Body wall scales, including marginals, are somewhat crescent-shaped, wider than tall (H:W = 0.6-0.7), and slightly curved to accommodate the curvature of the polyp, the distalmost scales in each row (the marginals) having a straight or slightly rounded, finely serrate distal margin, projecting only about 10-20 µm beyond the articulation with the base of the operculars, and, if rounded, producing a slightly scalloped calyx margin. The 8 opercular scales are similarly-shaped (H:W = 1.5-1.9), symmetrical, isosceles triangles, having an apical angle of 41°-51° but with rounded tips. The abaxial operculars are up to 0.42 mm in height, the adaxials about 0.30 mm in height. The upper surface of the each opercular is covered with small spines on the lower half and 3 or 4 longitudinal ridges apically. The lower two-thirds of the undersurface is covered with complex tubercles of the same size as those of the body wall scales: the distal region is smooth, not keeled. The lateral edges of each opercular is finely serrate like the distal edges of the body wall scales. The 8 opercular scales fold together forming a moderately tall, conical operculum.

Coenenchymal scales occur in one layer, are flat, and elliptical to elongate in shape, the largest scales being 0.40 mm in length. Like the other scales, they are sparsely granular above, tuberculate below, and bear finely serrate edges. Tentacular sclerites were not noted.

Comparisons.-See Table 1.

Distribution.—Typical form: Blake Plateau from North Carolina (34°45'N) through Straits of Florida (insular side) and north central part of Cuba; 196–882 m. Forma robusta: Blake Plateau from off N. Car-

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olina (34°15'N) through Straits of Florida to Florida Keys; 183–877 m. Forma *obtusa*: Blake Plateau from off Georgia (31°27) through Straits of Florida and Northwest Providence Channel; 183–743 m.

Remarks.-Deichmann (1936) described a variety of P. pourtalesii called robusta, which differs from the typical form in having a stouter corallum, thicker sclerites, a flatter operculum, and longitudinal ridges on the opercular scales. This form is well represented in our collection (listed separately above), and differs from the typical form (Table 1) in having a stouter, stiffer colony, and slightly larger and thicker polvps (1.0-1.2 mm tall, 0.65 mm in diameter) that are more closely spaced on the branch (distance between adjacent polyps on one side of a branch 0.5-0.8 mm), such that even though the polyps are slightly larger, there are more/cm, i.e., 14-16, the latter number achieved when polyps also bud from the anterior face of the branch. As Deichmann stated, in general, the operculum is flatter, even concave in some highly contracted polyps, but both forms have longitudinal ridges on the opercu'ar scales. These several differences are fairly consistent but do not include any characters routinely used to differentiate species of Plumarella (see Kükenthal 1919). Furthermore, the distribution and bathymetric range of both taxa are virtually the same, 7 of the 22 records of robusta being from common stations. We thus concur with Deichmann in considering this form as just an environmental variation of the typical form.

Another common form of *P. pourtalesii*, represented in our collection by 27 lots, is otherwise similar to forma *robusta* but differs in that the marginal scales of at least some polyps of every colony have an angled or ever pointed distal edge (Fig. 2D). The angle o'the distal edge is often a sharp right angle extending about 0.1 mm, or less commonly may be a discrete spine up to 0.25 mm in length. There is great variation in the expression of this character. In some colonies all marginal scales of all polyps will have a short angled distal edge, whereas in other colonies only those polyps toward the distal branch tips will be so modified, the marginal scales of the remaining polyps having a typically straight or rounded edge. Furthermore, individual polyps may have one or all eight marginal scales with an angled edge. The long-spined marginals are infrequent and when present only occur one to a polyp. All three forms sometimes occur at the same station, and their bathymetric and geographic ranges are quite similar. Because of the great variation of this single character that separates this taxon from forma robusta and the typical form, it is considered to be an environmental or genetic variation without taxonomic validity, but, in order to easily refer to this variation, the form name obtusa is applied to it, an allusion to the often obtuse angle formed by the distal edges of its marginal spines.

Plumarella pellucida, n. sp. Figs. 3D-F, 4A-B, 10A

Material examined/types and type locality.—Holot pe: G-647, 1 colony and SEM stubs C1079–1080, 1085–1086, USNM 52992. Paratypes: Alb-III 9-19, 1 colony, USNM 50573; Cape Hatteras SA6-5, 2 colonies, USNM 1019404; Cr266, 3 colonies, USNM 59506; G-647, 2 colonies, 3 branches, USNM 1019403; G-808, 1 colony, USNM 59499; G-859, 3 branches and 1 unnumbered SEM stub, USNM 52993; O-11705, 5 branches, USNM 1019405. Type Locality: 26°16'N, 79°43'W (Straits of Flort Lauderdale), 520–549 m.

Diagnosis.—Distal edge of marginal scales rounded or straight; branching closely pinnate, branchlets of moderate length and stiff; opercular scales granular but not ridged, other scales faintly granular, appearing almost smooth and translucent; abaxial and outer-lateral opercular scales quite long and curved; 10–12 polyps/cm.

Description .- Colonies are flabellate and



closely pinnately branched, as in *P. pourtalesii*, the distance between successive branchlets 2.5–5.0 mm, and the entire flabellum is usually convexly shaped, the polyps curving toward the convex (anterior) face. Branchlets are up to 60 mm long and are fairly stiff. The main stem is anchored by a dense calcareous holdfast. The axis is yellow and faintly longitudinally striate; in alcohol the colony is light brown. The largest colony (holotype) is 17 cm in height, 16 cm in width, and 2.2 mm in basal stem diameter.

Polyps are quite regularly arranged in a biserial, alternating fashion on all branch edges, and are inclined distally. Polyps on the same side of a branchlet are well separated by 1.0–1.2 mm, resulting in 10–12 polyps/cm. Polyps are 1.1–1.2 mm in height and slightly flared distally (0.65 mm in diameter).

Each polyp is covered with 8 opercular and 8 rows of body wall scales, the abaxial body wall scales numbering about 6, the adaxial usually consisting of 5. The body wall scales, including the marginals, are similar in size and shape to those of P. pourtalesii; however, their exterior granulation is much reduced and the scales appear to be thinner, producing a smooth, almost translucent aspect. Like P. pourtalesii, the distal edges of the marginals are straight to slightly rounded, never spinose or angled. The 8 opercular scales are isosceles triangles (H:W = 1.7-2.4), having an apical angle of 20°-35°, ranging from sharply pointed to slightly rounded. The abaxial and outer-lateral operculars measure up to 0.54 mm in height, the adaxial and inner-lateral operculars only 0.37 mm in height. The distal third of the abaxial and outer-lateral operculars are attenuate, with slightly serrate edges; these scales are curved downward to follow the curvature of the polyp and almost reach the opposite side of the polyp, considerably overlapping the shorter adaxial and innerlateral opercular scales. The opercular scales bear low sparse granules, lack distal ridges, and are tuberculate on the undersurface with no trace of a keel. In general, the opercular scales fold together in a conical operculum in a manner similar to that shown in Fig. 9f, the abaxial opercular having two exposed edges, the adaxial having none.

Coenenchymal scales occur in one imbricating layer, are flat, and elliptical to irregular in shape, the largest being about 0.41 mm in width. Their granulation is reduced similar to that on the opercular scales. Tentacular scales were not noted. All sclerite types, body wall, opercular and coenenchymal bear complex tubercles on their undersurfaces, the largest of which measures about 13 µm in diameter.

Etymology.-The species name pellucida (Latin: pellucidus, transparent, translucent, clear) refers to the translucent nature of the body wall and coenenchymal scales when viewed in liquid, probably due to their thinness and sparse granulation, which allows a view of the outline of the branch axis and of 8 faint white longitudinal lines in the polyps corresponding to the mesenteries.

Comparisons .- Plumarella pellucida belongs to a closely related species complex characterized by having large, pinnately branched colonies and smooth to straightedged (not spinose or pointed) marginal scales, this complex consisting of: P. pourtalesii, P. laxiramosa, and P. pellucida. It is probably most closely related to P. pourtalesii, but is distinguished by having nonridged opercular scales, the adaxial and outer-laterals of which are quite long and curved; and smooth, almost translucent body wall and coenenchymal scales. It differs from P. laxiramosa in having closer pinnate branching; longer, more attenuate opercular scales that are granular; and fewer polyps/cm. (Table 1). All three species occur in roughly the same geographic and bathymetric range and often occur at the same stations.

Distribution.---North Carolina through Straits of Florida, Bahamas; 549-1160 m.

Plumarella laxiramosa, n. sp. Figs. 4C-E, 5A-E, 10B

Material examined/types and type locality.-Holotype: Cape Hatteras SA6-1, 1 colony and SEM stubs C1081-1083, USNM 1019406, Paratypes: Alb-2416, 7 colonies, over 50 branches and 1 unnumbered SEM stub, USNM 50594 and 79458; Atl-266-41, 1 branch, USNM 1019407; Cape Hatteras SA6-1, 19 branches, USNM 79778; Cape Hatteras SA6-5, 8 colonies, USNM 79779; Combat 368, 1 branch, USNM 1019408; Gos-2387, 1 colony, 1019409. USNM Type Locality: 31°17'18"N, 79°00'39"W (Charleston Bump region, South Carolina), 572-575 m.

Diagnosis.—Distal edge of marginal scales rounded or straight; branching loosely pinnate, branchlets long and flabby; body wall, opercular, and coenenchymal scales smooth; 14–21 polyps/cm, polyps often occurring on anterior face.

Description .- Colonies are flabellate and pinnately branched, as in P. pourtalesii, but differ from that species in having more widely-spaced (loose pinnate) and thus fewer branchlets, each branchlet separated form their adjacent by 6-11 mm. Also, unlike P. pourtalesii, this species has flat, not curved, colonies, and its branchlets are longer (up to 80 mm) and less stiff, altogether producing a limp or languid colony tension. The main stem is anchored by a dense, white calcareous holdfast, which often attaches to the corallum of a dead scleractinian or stylasterid coral with an encrustation up to 1 cm in diameter. The axis is golden-yellow and faintly longitudinally striate; overall the colony is light brown in alcohol. The holotype is 18 cm in height, 17 cm in width, and has a main stem diameter of 2.7 mm. although the stem is broken from the substrate. The largest colony, which has an intact base (Alb-2416), is 24 cm in height.

Polyps are closely arranged on all branches biserially in the plane of the flabellum and in an alternating fashion; however, most larger colonies often have a third row of polyps on the anterior side, which produces a very crowded arrangement of polyps that may number up to 21/cm. Up to 20 polyps may occur on the rather lengthy internodes of the main and primary branches. Polyps are 1.1–1.2 mm in height and are slightly flared distally (0.65 mm).

Each polyp is covered with 8 opercular and 8 orderly rows of body wall scales, the abaxial body wall scales numbering 6 or 7/ row, the adaxial consisting of usually only 5. Body wall scales are roughly rectangular and slightly curved to fit around a segment of the polyp; the distalmost body wall scales (the marginals) are 0.30-0.34 mm in width and 0.20-0.25 mm in height, the scales becoming progressively smaller toward the branch. The distal edges of the marginals are finely serrate and straight to slightly rounded, never pointed or spinose. The undersurfaces of all scales are tuberculate (tubercles 12-26 um in diameter). whereas the upper surfaces of the body wall scales, as well as those of the opercular and coenenchymal scales, are virtually smooth. The 8 opercular scales are similarly-shaped (H:W = 1.75-2.20), symmetrical, isosceles triangles, having a blunt, rounded apical angle of about 30°. The abaxial operculars are up to 0.45 mm in height, the adaxials only slightly less tall (e.g., 0.37 mm). As mentioned above, the surface of the operculars is smooth and without ridges, whereas their undersurface is tuberculate. When contracted, the operculars form a closely fitted, overlapping, low operculum.

Coenenchymal scales occur in one imbricating layer, are flat, and elliptical to irregular in shape, the largest scales being about 0.25 mm in length. Tentacular scales were not noted.

Etymology.—The species name laxiramosa (Latin: laxus, loose, slack, and ramosus, branching) refers to the loose branching mode of the colonies as wells as the limp tension of the branchlets.

Comparisons.—Among those western Atlantic species of *Plumarella* having smooth-edged marginal scales (Table 1), *P*.

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Fig. 5. A-E, Plumarella laxiramosa, holotype: A, upper and undersurfaces of 4 opercular scales; B, tip of undersurface of an opercular showing fine serration of edge; C, upper and undersurfaces of 3 body wall scales; D, tubercles on underside of a body wall scale; E, upper and undersurfaces of 4 coencenchymal scales. F--I, Plumarella dichoroma, holotype: F upper and undersurfaces of 4 opercular scales; G, tubercles on underside of an opercular scale; H, upper and undersurfaces of 4 opercular scales; G, tubercles on underside of an opercular scale; H, upper and undersurfaces of 5 body wall scales; I, upper and undersurfaces of 5 coenenchymal scales. Scale bars for A, C, E-E, H-I = 0.10 mm; B = 25 µm; D, G = 10 µm.

laxiramosa is most easily distinguished by its growth form (loose pinnate) and by having a third, anterior row of branchlet polyps, which leads to a high number of polyps/cm. It is also distinguished by having no surface granulation on any scales.

Distribution.—Off North Carolina (to 34°15'N) and South Carolina; 348–625 m.

Plumarella dichotoma, n. sp. Figs. 5F-I, 6A-C, 10C

Material examined/types and type locality .- Holotype, Gos-2387, 1 colony and SEM stubs C1087-1089, USNM 57307. Paratypes: Alb-2666, 10 colonies, USNM 49423; Alb-2667, 9 colonies, USNM 49431; Alvin 77-762, 1 colony, USNM 1019427; Alvin 1335, 1 dry colony, USNM 73739; Anton Dohrn 65-32, 3 dry branches, USNM 1019429; Cape Hatteras SA6-5, 5 colonies, USNM 79780; Eastward 26004, 2 colonies, USNM 1019430; Eastward 26023, 1 colony, USNM 1019431; G-169, 2 colonies, USNM 52990; G-170, 1 colony, USNM 52996; Gos-2344, 3 colonies, USNM 58447; Gos-2387, 10 colonies, USNM 1019428: Gos-2413, 7 colonies, USNM 1019432; Gos-2469, 1 colony, USNM 59021. Type Locality: 31°14'48"N, 78°59'W (off South Carolina), 530 m.

Diagnosis.—Distal edge of marginal scales straight or rounded; branching dichotomous, sometimes lyrate, branchlets relatively short and wiry; opercular and body wall scales smooth; 8–10 polyps/cm (polyps widely spaced), standing perpendicular to branches on large-diameter branchlets.

Description—Colonies are flabellate and usually slightly curved, as in *P. pourtalesii*, but consistently dichotomously branched. The main stem is attached to a substrate by a thin calcareous encrustation and rises only 12-16 mm before it bifurcates, producing an axil angle of 65°-85°. Subsequent equal, dichotomous branching occurs at intervals of 5-12 mm, although some end branches are up to 40 mm in length and are the result of 7-11 previous branching nodes. Terminal branchlets are wiry to limp in tension. Higher order axil angles are slightly smaller, i.e., 40°-45°, undamaged colonies usually being slightly broader than tall. In some large colonies the two outermost branches remain slightly larger than their inner branchlets (unequal dichotomous branching), as in the holotype, producing a lyrate form. The largest colony (the holotype) is 11 cm in height, 13 cm in width. and has a basal main stem diameter of 1.4 mm, although most colonies examined were considerably smaller. The axis is golden yellow and the colony appears white in alcohol.

As in all species of *Plumarella*, the polyps are biserially arranged in alternating fashion on the edges of all branches, angled slightly toward the anterior side of the flabellum, and standing perpendicular to large-diameter branches, but inclined distally in smaller-diameter distal branches. Polyps are widely spaced, adjacent polyps on the same side of a branch separated by as much as 2.0 mm. Polyps are fairly tall and slender, up to 1.3 mm in height and 0.65 mm in apical diameter.

The polyps are protected by 8 opercular and 8 rather disorganized rows of body wall scales, both ab- and adaxial rows containing 5 or 6 scales. Body wall scales are smooth, quickly decreasing in size from the marginal to the more proximal ones. The distal edges of the marginals are straight to slightly rounded and the scales themselves are square to slightly rectangular. The opercular scales are modified isosceles triangles (almost pentagonal), the two long sides of the triangle being parallel for much of the length, only the distal third having an apical angle of 45°-50°, culminating in a blunt tip. Abaxial opercular scales are up to 0.50 mm in height, adaxial, 0.35 mm; the H:W ranges from 1.7-2.3. Operculars have a granular upper surface and a tuberculate lower surface, devoid of a keel. They infold to form an operculum as illustrated in Fig 9f.

Coenenchymal scales are mildly granular



above, tuberculate below, and irregularly elliptical in shape, rarely over 0.25 mm in greater diameter.

Etymology.—The species name dichotoma (Greek: to be divided into two parts), is an allusion to the dichotomous branching of the colonies.

Comparisons.—Among the western Atlantic species of *Plumarella*, *P. dichotoma* is unique in having both dichotomous branching and smooth-edged marginal scales (Table 1). It is also distinctive in having such widely spaced polyps that are often oriented perpendicular to the branches.

Distribution.—Off southeast coast of United States from South Carolina to off Dry Tortugas, Florida; 494–1065 m.

Plumarella aurea (Deichmann, 1936) Figs. 1C, 6D–E, 7A–D

- Thouarella aurea Deichmann, 1936:165– 166, pl. 25, figs. 12–13, pl. 26, fig. 11.— Bayer, 1954a:281 (listed).
- Plumarella pourtalesii.—Deichmann, 1936:156 (in part: 2 of 4 specimens from Bibb 22, Bahia Honda).
- Plumarella aurea.—Bayer, 1981:934, fig. 70 (new combination).—Bayer & Cairns (Verrill), 2004: pl. 25, 6a, pl. 83, 1a.

Material examined.-Alb-2666, 4 colonies, USNM 52984; Alb-2667, 5 colonies and 1 unnumbered SEM stub, USNM 52985; Alb-2668, 4 branches, USNM 1019312; Alvin 77-762, 3 colonies, USNM 1019313; Atl-3780, 15 dry colonies, MCZ; Atl-3782, 1 dry colony, MCZ 54327; Atl-266-40, 5 colonies and SEM stub 390, USNM 58443; Atl-266-41, 5 colonies, USNM 1019314; Cape Hatteras SA 6-5, 2 colonies, USNM 1019315; Discoverer X, 1 colony and SEM stub 391, USNM 58446; Eastward 26004, 1 colony, USNM 1019316; Eastward 26022, 2 branches, USNM 1019317; Eastward 26023, 4 dry branches and 1 in alcohol, USNM 1019318; G-672, 1 colony, USNM 52974; G-679, 1 colony, USNM 1019319; G-936, 1 branch, USNM 1019320; Gos-2385, 4 colonies and SEM stub C1092, USNM 56892; Gos-2414, 6 colonies, USNM 1019321; O-11716, 1 colony, USNM 59500; P-105, 3 colonies, USNM 52976; SB-453, 1 colony, USNM 51265; syntypes (see below); specimens misidentified as P. pourtalesii by Deichmann (1936) from the type locality, Bibb 22 (MCZ 59442).

Types and type locality.—Five small branches (syntypes) preserved in alcohol are deposited at the MCZ (4801), which also bear Verrill's number 8042. An unnumbered SEM stub of one of these branches is also deposited at the USNM. Type Locality: $24^{\circ}14'20''N$, $80^{\circ}59'40''W$ (off Bahia Honda, Straits of Florida off Florida Keys), 310 fathoms (=567 m). Although not stated in the original description, a label with the type specimens indicates they were collected at *Bibb* 22 (dredge 12), made on 4 May 1868.

Diagnosis.—Distal edge of most marginal scales prominently spinose; branching dichotomous; opercular, body wall, and coenenchymal scales smooth; polyps crowded, sometimes on anterior face, 14–22 polyps/ cm.

Description .--- Colonies are flabellate and dichotomously branched. The main stem is attached to the substrate by a thin calcareous expansion and rises only 5-8 mm before it bifurcates, producing an axil angle of about 55°; subsequent axial angles are 40°-45°. Branching is usually equal and dichotomous, occurring at intervals of 5-10 mm, but some terminal branches are up to 10 cm in length. Branches and colonies are quite flexible in tension, almost limp. The largest colony examined (Gos-2385) is 13 cm in height, 12 cm in width, and has a main stem diameter of 1.5 mm. The axis is golden-vellow and the colony appears white in alcohol.

Polyps are crowded, occurring biserially in alternating or opposite fashion on the branchlets and often with occasional polyps on the anterior side, resulting in 14–22 polyps/cm. Polyps are oriented perpendicular to the branches or tilted only slightly anteVOLUME 117, NUMBER 4



Fig. 7. A–D, Plumarella aurea, Gos-2385: A, upper and undersurfaces of 3 opercular scales; B, upper and undersurfaces of 2 marginal scales; C, upper and undersurfaces of 4 body wall scales; D, upper and undersurfaces of 4 coenenchymal scales. E–I, Plumarella aculeata, paratype from G-252: E, upper and undersurfaces of 2 opercular scales; F, upper and undersurfaces of 2 marginal scales; G, spination on marginal spine; H, upper and undersurfaces of 5 body wall scales; I, upper and undersurfaces of 5 coenenchymal scales. Scale bars for A–F; H–I = 0.10 mm; G = 25 µm.

riorly. They are usually squat, cylindrical, and robust, 0.8–1.2 mm in height (depending on contraction) but always 0.75–0.80 mm in apical diameter.

Each polyp is protected by 8 opercular and 8 well-defined rows of body wall scales, the abaxial rows having 6 or 7 scales, the adaxial, 5 or 6. The distal edges of the marginal body wall scales are usually strongly spinose, the 8 tooth-like spines forming a small crown encircling the operculum and often rising above it. Occasionally 1 or 2 of the marginals of a polyp lack spines or have reduced spines, but most polyps have 8 prominent, equal-sized spines. The marginal spines are sharp (apical angle 20°-25°), often constituting half the height of the marginal scale, a large spine being up to 0.25 mm in length and 0.08 mm in basal diameter, contributing to a H:W for this kind of scale of up to 1.3-1.5, the low value due to the wide base of the marginal scales. The marginal spines are circular in cross section and have finely serrate edges where they join the lower rectangular section of the scale (Fig. 7B). Opercular scales are fairly flat (not curved) and isosceles triangular in shape, the distal point being somewhat rounded, forming an angle of 33°-45°. Abaxial opercular scales are up to 0.55 mm in height, adaxial only 0.30 mm; the H:W ranges from 1.5-2.0. The upper surfaces of the body wall and opercular scales are smooth, the undersurfaces covered with complex tubercles that are up to 15-16 µm in diameter.

Coenenchymal scales are also smooth above, tuberculate below, and irregularly elliptical, elongate, or circular in shape; and up to 0.40 mm in greater diameter.

Comparisons.—Among the western Atlantic Plumarella having spinose marginal scales, P. aurea is most similar to P. aculeata (see that description and Table 1).

Distribution.—Blake Plateau from off South Carolina (32°10'N) through Straits of Florida to off Bahia Honda; Northwest Providence Channel, Bahamas; 310–878 m.

Plumarella aculeata, n. sp. Figs. 7E-I, 8A-B, 9a-g, 10E

Material examined/types and type locality .--- Holotype: G-707, USNM 52980, 1 dichotomous colony and SEM 248. Paratypes: Cape Florida X, 11 pinnate colonies, USNM 1019533; Eastward 26535, 15 pinnate branches, USNM 1019534; Eastward 26547, 2 dichotomous colonies, USNM 1019535; G-241, 1 pinnate branch, USNM 1019536; G-252, 2 pinnate branches and SEM stubs 255 and C1090, USNM 52979; G-633, 2 pinnate colonies, USNM 52983; G-692, 8 pinnate colonies, USNM 52986; G-695, 1 dichotomous colony, USNM 52978; G-707, 5 dichotomous and 1 lyrate colonies, USNM 52981-52982; G-1125, 3 pinnate colonies, USNM 52977; G-1312, 1 lyrate colony, USNM 52975; SB-440, 4 dry pinnate branches, USNM 51292. Type Locality: 26°27'N, 78°40'W (Northwest Providence Channel, Bahamas), 514-586 m.

Diagnosis.—Distal edges of 4–7 marginal scales prominently spinose, the spines corresponding to those opercular scales that have one or both of their edges overlapped by flanking opercular scales; branching variable, including dichotomous, close-pinnate, and lyrate; all scales covered with a low, often inconspicuous, granulation; 10– 12 perpendicularly oriented polyps/cm.

Description .- Colonies are flabellate. slightly convex, and occur in three branching forms: dichotomous, lyrate, and closepinnate. The most commonly collected form is close-pinnate, colonies up to 12 cm in height and 11 cm in width, with a basal branch diameter of 1.7 mm, and consisting of 4 or 5 distinct plumes. Internodes are only 3-5 mm apart, producing a series of closely spaced, parallel, wiry branches that rarely exceed 4 cm in length. Dichotomous colonies are usually smaller, the holotype only 6 cm tall, 7.5 cm in width, and having a basal stem diameter of 0.8 mm. The first bifurcation occurs 7-11 mm above the substrate; subsequent branching occurs every 3-10 mm, distal branchlet rarely more than





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Fig. 9. Diagrammatic representation of seven arrangements (a-g) of marginal and opercular scales in *Plumarella acultata*, as viewed from above the operculum. The eight large triangles of each figure are the 8 operculars; the smaller triangles are the corresponding marginal scale spines. The numbers on the operculars indicate how many of its two edges overlap an adjacent opercular, the arrows also indicating which edge overlaps an adjacent opercular, the arrows also indicating which edge overlaps an adjacent opercular, the arrows also indicating which edge overlaps an adjacent opercular spinal scales corresponding to operculars having one or both of its edges overlapped by an adjacent opercular; marginal corresponding to operculars that are overlapped by both adjacent operculars of not how the spine.

3 cm. The lyrate form is believed to be a variation of the dichotomous form. The axis is yellow-gold; polyps (in alcohol) are white.

Polyps are arranged biserially in the plane of the flabellum in an alternating fashion and are well spaced (1 mm apart), resulting in 10–12 polyps/cm. Polyps are oriented away from the convex side of the flabellum (toward the anterior side) and usually perpendicular to the branchlet. Polyps are distally flared, and including the elongate marginal spines, measure up to 1.8 mm in height and 0.7–0.8 mm in distal diameter.

Each polyp is protected by 8 operculars and 8 rows of body wall scales, both aband adaxial rows having the same number of scales (3 or 4) as the polyp is not curved toward the branch. Four to seven (usually 5 or 6) of the marginal scales bear extremely long, slender, sharp (apical angle 8° –10°) spines, that are cylindrical in cross section. They are slightly curved over the polyp face and often lack granulation, thus appearing translucent, or may be covered with aligned spinules (Fig. 7G). The spine portion of the marginal scales constitutes 60-65% of the length of the scale, resulting in a H:W of 1.8-2.8. The basal portion of the spined marginals is massive: rounded or shield-shaped. The number and position of marginal spines appears to be directly correlated to the corresponding opercular scales that have one or both of their edges overlapped by flanking opercular scales. Opercular scales that overlap both adjacent operculars do not have a corresponding spinose marginal, their distal margins being only slightly rounded. Because every polyp has 8 operculars and thus 16 opercular edges, and every edge must either overlap or be overlapped by an adjacent opercular, it is mathematically possible for 4 to 8 operculars to have one or two edges overlapped, resulting in a polyp with 4-8 marginal spines (Fig. 9). Polyps having only 4-7 marginal spines have been observed; the



Fig. 10. A. Plumarella pellucida, holotype; B, P. laxiramosa, holotype; C, P. dichotoma, holotype; D, Candidella imbricata, Gos-2384; E, Plumarella aculeata, holotype; F, Acanthoprimnoa goesi, Ad-3465, MCZ 3741. Scale bars for A, B, F = 5 cm; C-E = 2.5 cm.

hypothetical 8-spined polyp has not been seen. Body wall scales of the second and third tier are large, thick, rectangular, and have rounded upper edges; they are smooth or bear only low granules. The fourth tier of scales consists of small scales indistinguishable from the coenenchymal scales. The opercular scales are isosceles triangular in shape with a broad base and attenuate rounded tips that form an apical angle of $20^{\circ}-25^{\circ}$; their edges are finely serrate and their upper surface smooth to inconspicuously granular. Operculars are up to 0.62 mm in height and have a narrow range of H:W of 1.6–2.2.

Coenenchymal scales are flat, irregular in shape, 0.20–0.40 mm in width or diameter, and have a conspicuously granular upper surface. The undersurface of all scales and the upper proximal sides of most where the scale is overlapped by an adjacent scale, are covered with complex tubercles up to 18 µm in diameter.

Etymology.—The species name aculeata (Latin: aculeatus, sharp-pointed) is an allusion to the extremely long, sharp-pointed spines of the marginal scales.

Comparisons.—Six species of Plumarella are characterized by having spinose marginal spinos (Kükenthal 1919); four of those six endemic to Japan. Plumarella aculeatus differs from these in having extremely elongate and sharp marginal spines that occur only on those marginal scales that correspond to opercular scales that have overlapped margins (Figs. 88, 9).

Distribution.—Insular northern Straits of Florida; Northwest Providence Channel, Bahamas; 400–900 m.

Acanthoprimnoa, n. gen.

Type species.—Plumarella goesi Aurivillius, 1931, here designated.

Diagnosis.—Primnoidae with a well-defined operculum; polyps usually inclined apically, each completely surrounded by 8 rows of body wall scales; polyps arranged alternately and biserially; 8 marginal scales, each with a spinose or finely serrate (pectinate) distal margin; no sclerites bear tubercles on their under surfaces; opercular scales not keeled; colonies uniplanar, usually pinnately branched (plumose), dichotomous, or lyrate. Brooding polyps are common.

Distribution.—Straits of Florida, Bahamas, Yucatan Peninsula, Lesser Antilles; Japan; 60–1125 m.

Remarks .--- In his unpublished manuscript on the western Atlantic deep-water octocorals (Bayer & Cairns 2004), Verrill referred to the type species of this genus as Acanthoprimnoa aspera, a species later described by Aurivillius as Plumarella goesi. Because only Verrill's plates and not the text survived we do not know what criteria he used to distinguish his new genus. We separate this genus from the morphologically similar Plumarella by three criteria: the lack of tubercles on the undersurfaces of the sclerites, the distinctive pectinate distal edges of the body wall and opercular scales, and the coarsely granular coenenchymal scales. Two other species, previously placed in Plumarella, also share these characteristics and are transferred to Acanthoprimnoa: A. serta (Kükenthal & Gorzawsky, 1908), n. comb. and A. cristata (Kükenthal & Gorzawsky, 1908), n. comb.

Etymology.—The genus name Acanthoprinnoa (Greek: acantha, a thorn + primnoa, a common suffix used in this family) is an allusion to the spiny nature of the polyps of the type species.

Acanthoprimnoa goesi (Aurivillius, 1931), n. comb.

Figs. 8C-D, 10F, 11A-I, 12A-B

- ?Primnoa Pourtalesii.—Hargitt & Rogers, 1901:281, fig. D.
- *Plumarella goësi* Aurivillius, 1931:244– 248, pl. 5, figs. 6a–b, text fig. 47, 3–5.— Bayer, 1957:388 (Cay Sal Bank).
- *Thouarella goësi* Deichmann, 1936:164– 165, pl. 25, figs. 2, 19–23, pl. 26, fig. 8.—Bayer, 1954a:281 (listed).



Fig. 11. A–I, Acanthoprinnoa goesi, G-633: A, upper and undersurfaces of 3 opercular scales; B, pactinate edge of an opercular; C–D, under and upper surfaces of 2 marginal scales; E, upper and undersurfaces of 3 coarsely granular coenenchymal scales, F having a central spine: I, granules on upper surface of a coenenchymal scale. J–M, Acanthoprinnoa pectinata, holotype: J, upper and undersurfaces of 3 coarsely granular coenenchymal scales; T, upper and undersurfaces of 4 butterfly-shaped body wall scales; L, upper and undersurfaces of 3 opercular scales; K, upper and undersurfaces of 4 butterfly-shaped body wall scales; L, upper and undersurfaces of 3 coarsely granular coenenchymal scales; M, coenenchymal scales on a branch. Scale bars for A, C–H, J–K, M = 0.10 mm; B, I, L = 25 μm.



"Acanthoprimnoa aspera" Bayer & Cairns (Verrill), 2004: pl. 10, fig. 8, pl. 13, fig. 8a, pl. 27, figs. 5a–b, pl. 141, fig. 6.

Material examined .- Alb-2342, 10 dry pinnate colonies, USNM 10236; Alb-2343, 1 pinnate colony, USNM 10243; Alb-2346, 1 pinnate colony, USNM 10783; Alvin 846, 3 dry pinnate colonies, USNM 79517; Alvin 77-764, 4 pinnate colonies, USNM 96825; Atl-2999, 10 dry pinnate branches, MCZ 54324 and 3832; Atl-3402, 4 dry pinnate branches, MCZ 3703; Atl-3403, 7 dry pinnate branches, MCZ 54335; Atl-3438, 3 dry pinnate branches, MCZ 3751; Atl-3463, 7 dry pinnate colonies, MCZ 3604; Atl-3465, 54 dry pinnate colonies, MCZ 3744a, 3741, and 3737; Atl-3466, 17 dry pinnate colonies, MCZ 3603; Atl-3478, 20 dry pinnate colonies, MCZ 3605; Atl-3479, 17 dry pinnate colonies, MCZ 3608 and 3759; Atl-3480, 11 dry pinnate colonies, MCZ 3668 and 3762; Atl-3482, 32 dry pinnate colonies, MCZ 3654 and 3663; Cape Florida X, 8 pinnate colonies, USNM 73932; JS-43, 6 pinnate colonies and 1 unnumbered SEM stub, USNM 43801; JS-102, 1 dry pinnate colony, USNM 1011364 (topotypic); JS-103, 3 pinnate colonies, USNM 50951 (topotypic); Eastward 26537, 2 pinnate (USNM 98161) and 13 dichotomous colonies (USNM 98850); Eastward 26538, 10 pinnate branches, USNM 1019537; Eastward 26549, 1 pinnate colony (USNM 75064) and 24 dichotomous colonies (USNM 75065, 76987, and 79485); Eastward 26550, 53 pinnate colonies, USNM 94500; Eastward 26559, 8 dichotomous (USNM 98851) and 1 pinnate colony (USNM 98852); Eastward 31281, 15 pinnate colonies, USNM 94522; G-235, 3 pinnate colonies, USNM 98853; G-241, 16 pinnate colonies, USNM 52966; G-242, 1 pinnate colony, USNM 52968; G-251, 2 pinnate colonies, USNM 52969; G-252, 1 pinnate branch, USNM 98854; G-254, 1 pinnate colony, USNM 52962; G-387, 12 pinnate colonies, USNM 52970; G-533, 1 pinnate colony, USNM 52971; G-633, 13 pinnate colonies and SEM stubs 258 and C1091, USNM 52973 and 52983; G-679, 8 pinnate colonies and SEM stub 256, USNM 52963; G-680, 4 dichotomous colonies, USNM 1019538; G-696, 1 pinnate colony, USNM 52972; G-704, 1 pinnate colony, USNM 52965; G-706, 25 pinnate colonies, USNM 52967: G-707, 1 pinnate colony, USNM 98855; G-879, 2 dichotomous colonies, USNM 76988; G-897, 10 dichotomous colonies and SEM stub 257, USNM 52964; P-594, over 50 pinnate colonies, USNM 52961, and 4 dichotomous colonies, USNM 98856; P-596, 2 dichotomous colonies, USNM 52960; P-598, 1 pinnate colony, USNM 52957 and 1 dichotomous colony, USNM 98858; specimens reported by Deichmann (1936) and Bayer (1957); a syntype (USNM 44192).

Types and type locality.—Three specimens are mentioned in the original description, only one of which was figured; all three are considered to be syntypes. They are deposited at the Stockholm Museum (#28); a fragment of one of the colonies is also deposited at the USNM (44192). Type Locality: "Virgin Islands", 457–548 m.

Diagnosis.—Distal edges of 7 marginals scales (not one of the adaxial marginals) prominently spinose; branching dichotomous in shallow-water form, branchites flexible but not flaccid; opercular scales covered with numerous tiny spines, abaxial and outer-lateral body wall scales bear single, robust spines on distal margin; coenenchymal scales highly granular and sometimes bear a single tall spine; 13–15 polyps/cm; branch axis bronze; polyp brood chambers common.

Description.—Colonies are flabellate and occur in two branching forms. The deeper water form is larger (up to 30 cm in height and equally broad), with closely pinnate branching colonies consisting of 2 or 3 regular plumes. Pinnate branchlets begins within 5 mm of the base and are subscquently arranged in a regular parallel fashion, the internodes being only 2–3 mm in length; unbranched terminal branchlets are flexible and rarely exceed 4 cm in length. These large colonies are attached by a calcareous holdfast that may reinforce the main stem as much as 15 mm above the base and attain a diameter of 4 mm. As with most species of Plumarella, the colony flabellum is slight convex, with the polyps directed slightly upward and toward the convex face. The shallow-water form is much smaller (rarely exceeding 4 cm in height) and is dichotomously branched, often resulting in a colony broader than tall. Internodes are 2-4 mm in length; terminal branchlets are rarely more than 15 mm and number only about 10-15; the basal axis is about 0.5 mm in diameter. In both forms the axis is a rich bronze color, which contrasts with the white (in alcohol) color of the polyps.

Polyps are arranged biserially in the plane of the flabellum in an alternating fashion and are well spaced approximately 0.6–0.8 mm apart, resulting in 13–15 polyps/cm. Polyps of the deep-water form are 0.8–1.2 mm in height (including the marginal spines) and about 0.5 mm in diameter; polyps of the shallow water form are smaller, usually less than 0.8 mm in height. As mentioned in the remarks section, some polyps of both forms have brood chambers that greatly swell the base of the polyp.

Each polyp is protected by 8 opercular and 8 rows of body wall scales, the abaxial row having 5 or 6 scales, the adaxial, 4 or 5. Seven of the 8 marginal body wall scales bear a prominent distal spine, the 8th (adaxial) marginal having a very reduced spine, allowing the abaxial opercular scales to overlap the polyp edge at that point of the circumference (Fig. 8D). The marginal scales have a flat, rectangular to ellipsoidal base up to 0.4 mm wide from which the elongate, sharp-tipped (apical angle 7°-8°), often crooked spine emerges. The entire marginal scale may be up to 0.85 mm in height, the spinose part constituting 75-85% of its height and contributing to a rather high H:W of 1.7-3.2. The elongate spinose part of each marginal scale is spinose itself, bearing prominent rows of smaller spines (25-30 µm in length), which are arranged in rows on both the upper and lower surface of the spine. The smaller spines also cover the edges and upper surfaces of the base of the marginals, but the undersurfaces of the marginal base, covered by tubercles in all species of Plumarella, is smooth. The body wall scales of the abaxial and innerlateral rows that lie proximal to the marginals also have apical spines, but these are quite variable in size, some quite large (up to half the height of the scale), others inconspicuous. The body wall scales of the adaxial and outer-lateral rows that lie proximal to the marginals have greatly reduced or no apical spines. The opercular scales are similar to the marginal scales in many ways but are isosceles triangular in shape, not having a rectangular base, and often have a notch on either side near the base. The abaxial operculars are quite elongate (up to 0.7 mm) and, when closed, often completely traverse the polyp. Their tips are pointed (apical angle 15°-25°), with a H:W ranging from 1.8-3.9. As with the marginal spines they are covered with prominent spines on the upper and undersurfaces, except for the undersurface of the base, which is smooth. All three edges of the opercular scales are serrate, but in the region of the proximal notches the serrations are developed into elongate (up to 40 µm long and 9 µm in diameter), finely granular pillars that often bi- and trifurcate (Figs. 11A-B).

Coenenchymal scales are rather large (up to 0.5 mm) and have coarse granular edges and surfaces, the granules rounded and up to 12 µm in diameter and often twice as tall. Some coenenchymal scales also bear aprominent, centrally located, perpendicular spine up to 0.3 mm in height and 0.1 mm in basal diameter. These spines are ormamented with smaller spines similar to those on the opercular and marginal scale spines. The undersurface of the coenenchymal scales is smooth.

Comparisons.-See A. pectinata.

Distribution.—Throughout the Straits of Florida to Arrowsmith Bank, Yucatan Channel; Northwest Providence Channel; Old Bahama Channel; Puerto Rico (Hargitt & Rogers 1901); Virgin Islands. In general, the dichotomous form occurs from 137–350 m and the pinnate form deeper, 320–595 m.

Remarks .- The only differences between the two forms, aside from their different range of capture depths, are that the deeperwater form has close pinnate branching, a larger colony, and larger polyps, whereas the shallow-water form has dichotomous branching, a smaller colony, and smaller polyp size. All other characters are quite similar, unique characters including the brooding polyps, spinose body wall and coenenchymal scales, and long, spiny operculars. Several stations contain both forms (see material examined), but in general the forms occur at different depth ranges. Some colonies are transitional in form, beginning as dichotomous but with a tendency toward pinnate branching at least in part of the upper colony. Such was the syntype illustrated by Aurivillius (1931: pl. 5, fig. 6a), although he unequivocally classified that colony as dichotomous.

About one-third of the colonies examined contained polyps with bulbous brood chambers in their base, this feature occurring in both the dichotomous and pinnate forms. Among the colonies containing polyps with brood chambers, approximately one in 50 polyps would be so modified, but oftentimes there would be 2 or 3 contiguous brooding polyps. There appears to be no seasonality regarding the presence of the brooding polyps.

Acanthoprimnoa pectinata, n. sp. Figs. 1D, 11J-M, 12C

Material examined/types and type locality.—Holotype: G-899, 1 colony and SEM stubs C1093–1095, USNM 1019539. Paratypes: Alb-2354, 20 colonies and 1 unnumbered SEM stub, USNM 43026 and 75112; Alvin 77-760, 5 dichotomous colonies, USNM 1019540; *Atl*-3303, 3 dry pinnate colonies, MCZ 3627; *G*-692, 2 branches and SEM stub 254, USNM 52954; *G*-889, 4 colonies, USNM 52952; *G*-898, 1 pinnate colony, USNM 52955; *G*-899, 19 colonies, USNM 52955; *O*-4940, 2 colonies, USNM 52953; *P*-592, 20 colonies, USNM 52958; *P*-954, 1 colony, USNM 52959; *SB*-5190, 6 pinnate colonies, USNM 1019541. Type Locality: 20°57'N, 86°34'W (off Arrowsmith Bank, Yucatan, Mexico), 40–164 m.

Diagnosis.—Distal edge of marginal scales straight or only slightly spinose; branching loosely pinnate, branchlets long and flaccid; opercular scales ridged and covered with numerous tiny spines; lateral edges of opercular and distal and proximal edges of body wall scales bear a series of comb-like spines; coenenchymal scales coarsely granular, but without a central boss; 11–13 polyps/cm; branch axis bronze; polyp brood chambers common.

Description .- Colonies are flabellate and loosely pinnate, each colony consisting of 2 or 3 plumes, although one colony (P-594) is lyrate in branching. The first branchlets occur very near the base of the colony, succeeding branchlets at a periodicity of every 4-5 mm (internode length), the branchlets up to 55 mm in length and flaccid in tension. The main stem is anchored by a dense, calcareous, white holdfast, although the holdfasts of only five of the colonies are intact. Like A. goesi, the axis is bronze in color, which contrasts with the white polyps. The holotype is 18 cm in height, 7 cm in width, but lacks a base; the largest specimen (Atl-3303) is 22 cm tall. The largest main stem of an attached colony (G-899) has a diameter of only 1.1 mm.

Polyps are arranged biserially on the branchlets and main stem (6-7) polyps/internode on main stem) in an alternating fashion 0.8–1.1 mm apart, resulting in 11–13 polyps/cm. Polyps are relatively small, only 0.8–0.9 mm in height and 0.40–0.45 mm in diameter. Colonies from all stations recorded contain some polyps with brood

chambers, which greatly swell the base of those polyps.

Each polyp is protected by 8 opercular and 8 rows of body wall scales, the abaxial row consisting of 8-10 scales, the adaxial, 7-9. All body wall scales, including the marginals, are slightly curved to accommodate the curvature of the polyp, and considerably wider than tall, such that a relatively high number occurs in the wall of a relatively short polyp. The upper surface of the body wall scales bears many small spines, especially toward the center of the scale, and their distal and proximal margins bear a series of fine, comb-like (pectinate) projections measuring up to 32 µm in length. Only rarely will the marginal body wall scale have a larger, projecting spine, the largest up to 0.25 mm in length and constituting about half the height of the scale. The opercular scales are isosceles triangular in shape (H:W = 1.6-2.2), and strongly curved in order to cover the top of the rounded polyp. Operculars are up to 0.38 mm in height and have an apical angle of 35°-45°. They are sculptured as in A. goesi.

Coenenchymal scales are relatively small (0.09–0.21 mm in width) and circular to irregular in shape. As in A. goesi, they are densely covered on their upper surface with prominent, blunt granules measuring up to 15 μ m in height and 10–12 μ m in diameter, but smooth on the undersurface.

Etymology.—The species name *pectinata* (Latin: *pectinatus*, comblike) refers to the comb-like serration of the edges of the opercular and body wall scales.

Comparisons.—Acanthoprimnoa pectinata resembles A. goesi in the morphology of its opercular spines, color of the branch axis, coarsely granular coenenchymal scales, and the common presence of brood polyps. Further, A. pectinata differs (Table 1) in lacking distally spinose body wall scales (instead having pectinate distal and proximal margins), lacking a central boss on the coenenchymal scales, having more scales/body wall row, having much shorter operculars, and in having a looser pinnate branching mode. *A. pectinata* is most similar to the Japanese *A. cristata*, but lacks the longitudinal ridges on the body wall scales.

Distribution.—Off northeastern Yucatan Peninsula and northwestern Cuba (164–476 m); Straits of Florida; Mona Passage and off Montserrat, Lesser Antilles (614–686 m).

Remarks.—All but two colonies of A, pectinata occur in relatively shallow water (164–476 m) off the Yucatan Peninsula, but the colonies from P-954 (off Montserrat, Lesser Antilles) and Alvin 77-760 (Straite of Florida) occur in deeper water (614–686 m) and are the only colonies to have nonpinnately (dichotomous, lyrate) branching colonies.

Genus Candidella Bayer, 1954

Primnoa.-Johnson, 1862:245 (in part).

- Stenella Gray, 1870:48 (junior primary homonym of Stenella Gray, 1866, a cetacean).—Wright & Studer, 1889;56 (in part).—Kükenthal, 1919:443–445 (in part); 1924:303 (in part).—Aurivillius, 1931:289–290 (in part).
- Narella.-Studer, 1878:643 (in part).
- Stenella (Primnoa).-Roule, 1896:304.
- Stenella (Stenella).-Versluys, 1906:38-39.
- Candidella Bayer, 1954b:296 (nom. nov.); 1981:937.—Tixier-Durivault, 1987:171.
- Candidella (Candidella).—Bayer, 1956: F222.

Type species.—Primnoa imbricata Johnson, 1862, by monotypy.

Diagnosis.—Primnoidae with a well-defined operculum; polyps stand perpendicular to branch (not bent); polyp body wall completely surrounded by 2–4 rows of sclerites; polyps arranged in whorls; only four marginal scales; undersurfaces of all sclerites tuberculate, opercular scales strongly keeled; colonies dichotomously branched in one plane.

Distribution.-North Atlantic, Ascension, central and western Pacific: 183-2139 m.

Remarks .- Four species are known in

this genus: C. imbricata (Johnson, 1862); C. johnsoni (Wright & Studer, 1889), Ascension: C. gigantea (Wright & Studer, 1889), Fiji: and C. helminthophora (Nutting, 1908), Hawaiian Islands. After its original description, the monographers Kükenthal, Studer, and Aurivillius took a broad view of the genus Stenella, including similar species but some differing in having 5 or 8 marginal scales, these species later being transferred to Parastenella, Pterostenella, and Dasystenella. Versluys (1906) was the first to relegate what is now known as Candidella to a monophyletic group, the nominate subgenus of Stenella. After renaming the genus Candidella (Bayer, 1954b), because the name Stenella was a junior homonym, Bayer (1956) also recognized it as a monophyletic subgenus: Candidella (Candidella), subsequently elevating it to generic rank in 1981. Characters used to distinguish species include the arrangement of polyps, colony branching, and polyp size (Kükenthal 1924).

Candidella imbricata (Johnson, 1862) Figs. 10D, 12D, 13A–G, 14A–D

- Primnoa imbricata Johnson, 1862:245, pl. 31, figs. 2, 2a (Madeira); 1863:299 (verbatim).
- Stenella imbricata.—Gray, 1870:48–49, 2 figs. (listed, new comb.).—Wright & Studer, 1889:56, 281 (listed).—Kükenthal, 1919:448-449 (Blake from Cuba, first record for western Atlantic); 1924:305–306 (diagnosis, key).—Thomson, 1927:32– 33, pl. 2, fig. 9, pl. 3, fig. 9, pl. 5, figs. 5–6 (Azores, Morocco).—Aurivillius, 1931:290 (mentioned).—Deichmann, 1936:167–168, pl. 26, fig. 5 (West Indies).—Bayer, 1954a:281 (listed for Gulf of Mexico); 1964:532 (Straits of Florida).
- Narella imbricata.—Studer, 1878:643 (listed, new comb.).
- ?Stenella (Primnoa) johnsoni.-Roule, 1896:304 (Gulf of Gascogne).
- Stenella (Primnoa) imbricata.—Roule, 1896:304 (comparison to C. johnsoni).

- Stenella (Stenella) imbricata.—Versluys, 1906:42–43, 44, fig. 46 (redescription of type, key to spp.)
- Candidella imbricata.—Bayer, 1954b:296 (new comb.).—Tixier-Durivault & d'Hondt, 1974;1412–1413.—Grasshoff, 1981:222, map 1 (mid-Atlantic Ridge sw of Azores); 1982a:738, maps 4, 20; 1982b:948–949, figs. 20–21.—Grasshoff & Zibrowius, 1983:119–120, 122, pl. 2, fig. 7 (mid-Atlantic Ridge), pl. 3, fig. 14 (Biscay Bay).—Carpine & Grasshoff, 1985:6 (frontispiece), 33 (Mus6e Océanographique de Monaco catalog numbers).—Pasternak, 1985:29 (Rockaway Seamount).—Pettibone, 1991:705, 707 (polychaete commensal).
- Candidella (Candidella) imbricata.—Bayer, 1956:F222, fig. 159-4b.
- Candidella johnsoni.—Bayer, 1981:934, fig. 74.
- Stenella "florida" Bayer & Cairns (Verrill), 2004: pl. 13, figs. 1, 1a, pl. 25, fig. 13ab, pl. 82, figs. 2, 2a, pl. 83, fig. 6, 6a.

Material examined.-Alb-2753, 3 branch fragments, USNM 44126; Alvin 762, 6 branches, USNM 80939, 80940, and 1017255; Alvin 1335, 2 fragments (one dry), USNM 73744 and 73745; Alvin 3885-5, 1 complete colony, USNM 1019238; Al-3903-101-2, 1 branch, USNM vin 1019273; Atl-266-47, branch fragments, USNM 60337; Atl-280-9, 3 branches and SEM stub 273, USNM 57552; CI-63, 1 colony, USNM 60223; CI-140, 1 branch, USNM 60341; Eastward 26019, 6 colonies, USNM 60338; Eastward 26022, 2 colonies, USNM 60340; Eastward 26023, dry branch fragments, USNM 1011365; Eastward 26031, 3 colonies (some dry) and SEM stubs 274 and C1071-1076, 1078, USNM 57553 and 60339; G-169, 6 colonies, USNM 52778; G-170, 2 colonies and 1 unnumbered SEM stub, USNM 52779; G-177, 2 colonies, USNM 52780; G-386, 14 colonies and numerous branches, USNM 52784; G-660, 1 branch, USNM 52781; G-661, 1 branch, USNM 52782; G-936, 2



Fig. 13. A–G, Candidella imbricata, Gos-26031: A, upper and undersurfaces of 4 opercular scales; B, tuberculate undersurface of an opercular; C, upper surface of 2 basal body wall scales; D, F, upper and undersurfaces of 3 medial body wall scales; E, undersurface of 2 marginal scales; G, upper and undersurfaces of 3 coenenchymal scales. Scale bars for A, C–G = 0.25 mm; B = 25 μ m.

branches, USNM 52783; G-965, 1 colony, USNM 52787; Gos-2383, 1 colony, USNM 57309; Gos-2384, 1 colony, USNM 57310; Gyre CO4, 1 colony (dry), USNM 57182; P-197, 2 colonies, USNM 52785; P-881, 2 colonies, USNM 52786; P-892, 2 colonies, USNM 52911; P-1146, 1 branch, USNM 52912; off Bermuda, 1200 m, 1 colony, USNM 75104.

Types and type locality.-The holotype

is deposited at the BM (1863.1.31.1). Type locality: Madeira, depth unknown.

Description.—Colonies consist of a robust vertical main stem up to 9 mm in basal diameter, which supports a uniplanar fan achieved by dichotomous branching. The main stem is anchored by a dense, white, encrusting, calcareous holdfast, which often encrusts other calcareous Coelenterata, such as the scleractinians *Enallopsammia pro-* VOLUME 117, NUMBER 4



funda, Lophelia prolifera, Javania cailetti, the stylasterid Stylaster erubescens, and various bryozoans. The calcareous deposits may reinforce the basal stem as much as 2 cm upwards from the base. The holdfast and basal reinforcement are composed of 100% aragonite, consistent with the findings of Bayer & Macintyre (2001) for the congeneric C. helminthophora. The axis is vellow-gold in color and longitudinally striate; overall the colony is white. The largest known colony (the holotype) is reputed to be 21.6 cm in height and 27.9 cm in width. Branching is dichotomous at intervals of 3-12 mm, but unequal, resulting in asymmetrical branching; there is little to no branch anastomosis.

Polyps are arranged in whorls of 3 or 4 polyps (rarely as pairs); if in a whorl of 3, 2 polyps are usually directed in the plane of the fan in opposite directions, the third polyp standing perpendicular to the plane of the fan and thus at 90° to the other 2, the polyp projecting perpendicular to the fan defining the anterior face of the fan; few polyps originate from the posterior face of the fan. When 4 polyps constitute a whorl, the angular separation between polyps is not 90°, but about 60°, polyps avoiding the posterior face. Polyp whorls are closely spaced, about every 1.2-2.0 mm, 5-6 occurring per cm, polyps present even on the calcified region of the basal stem and holdfast. Most polyps are 2.1-2.5 mm in height and slightly clavate (1.3-1.4 mm in distal diameter), encased by the distal margin of the flared marginal scales, but some geographic outliers have larger polyps (see Remarks). Polyps are fairly rigid, projecting perpendicularly from the branches; however, those in the plane of the fan are sometimes slightly curved toward the anterior face.

Polyps are protected by 4 marginal scales, 2–4 medial scales, 4–8 basal scales, and 8 operculars. The marginal scales are dimorphic in size and shape, consisting of 2 adjacent larger (0.9 mm in height, 1.1 mm in width), highly curved scales that define

the abaxial side of the polyp and 2 adjacent smaller (0.65 mm in height, 0.62 mm in width), slightly curved adaxial scales. which overlap with the edges of the larger marginals. Three opercular scales correspond to each of the larger marginals. whereas about 1.5 operculars correspond to the smaller marginals, the number of operculars adding to more than 8 because of the overlap of marginal scales. The marginals are flared outward distally, rising about 0.15 mm above the junction with the opercular scales, but not enclosing the operculum. Medial body wall scales are roughly rectangular and flat, with sides measuring 0.45-0.65 mm in length; their lateral edges overlap one another. Sometimes it appears that only 2 medial scales are present, these occurring on the adaxial side. Basal scales are dimorphic in size, consisting of 2 large, square to rectangular scales up to 0.65-0.70 mm in side length, and outwardly concave. as though squeezing the base of the polyp into a narrow opening. When polyps become abraded from the branches, these large scales often remain to mark the original position of the polyp. Between the 2 large basal scales, on the adaxial side, are 1 or 2 pairs of much smaller basal scales that are overlapped and overshadowed by the larger basals. The 8 operculars are elongate triangular, having a H:W of 1.6-2.0, pointed distally, highly convex above, and prominently keeled below. They form a tight conical operculum over the polyp, rising well above the marginal scales. One of the 8 operculars is slightly larger (e.g., 0.8 mm tall, 0.5 mm wide) than the others and is positioned opposite the smallest opercular (e.g., 0.6 mm tall, 0.3 mm wide), these two operculars defining the sagittal axis of the polyp. The remaining 6 operculars are of similar size, constituting 3 pairs mirrored across the sagittal axis. The 2 sagittal operculars are symmetrical, in that their keels are in a medial position, whereas the other 6 operculars are asymmetrical, their keels being offset toward the abaxial side (the side toward the large sagittal opercular),

producing a longer and slightly upturned edge of their adaxial side. Each upturned adaxial opercular edge overlaps the abaxial edges of the adjacent operculars, the edges of the small sagittal opercular being overlapped by both adjacent operculars and the large sagittal opercular overlapping both adjacent operculars (compare to Fig. 9f).

Coenenchymal scales are large (up to 1.0 mm in length), occur in one layer, are polygonal in shape, and are usually slightly concave above. As mentioned below, they sometime orient perpendicular to the branch in order to contribute to the formation of the worm tube. The upper surfaces of all sclerites are finely and uniformly granular, the granules 11–13 µm in diameter; their undersurfaces are covered with complex tubercles 15–17 µm in diameter. Tentacular sclerites were not noted.

Comparisons.—There is only one other species of Candidella known from the Atlantic, C. johnsoni (Wright & Studer, 1889), described from Ascension. As summarized by Versluys (1906), that species differs in having a very low operculum, marginal scales that are equal in size, and polyps that occur in pairs and singly. Although these two species are probably distinct, the only subsequent report of C. johnsoni is by Roule (1896) from the Gulf of Gascogne, which is probably C. imbricata, as he implied that his C. johnsoni might be a deep-water variety of C. imbricata.

Candidella inbricata is morphologically more similar to the central Pacific C. helminhophora (Nutting, 1908), both species having dimorphic marginal scales and a similarly shaped polyp. However, C. helminhophora differs in having two rings of medial body wall scales, a larger colony with longer internodes (up to 4 cm), larger polyps, and more flexible branches.

Distribution.—Western Atlantic: New England Seamounts (San Pablo, Rockaway, Kelvin, Muir), Bermuda, eastern coast of Florida, Bahamas, Greater and Lesser Antilles, northern Gulf of Mexico; 514–2063 m. A rather large distributional gap exists between the New England Seamounts and the coast of Florida. Eastern Atlantic: commonly collected in the Bay of Biscay, off Morocco, Canary Islands, Madeira, Azores, and the mid-Atlantic Ridge southwest of the Azores; 815–2139 m (see Grasshoff 1982b for map).

Remarks.-Colonies of even small size will usually host the commensal polynoid polychaete Gorgoniapolynoe caeciliae (Fauvel, 1913), larger colonies often hosting 5 or 6 worms. The polychaete has essentially the same known distribution as C. imbricata, despite the fact that it occurs in at least two other gorgonians (Pettibone 1991). The gorgonian appears to be induced to form a tube that is slightly elliptical in cross section, the greater diameter being approximately 2.3-2.5 mm and the length up to 25 mm, the tube always occurring on the anterior side of the fan; the length of the polychaete is about 11 mm. The tubes are formed predominantly of greatly enlarged and outwardly curved basal scales from two adjacent polyps. These basal scales, normally only 0.7 mm in height, increase in size up to 1.6 mm in height and up to 2.9 mm in width. The curvature is such that basal scales from two adjacent polyps in the same whorl meet and sometimes fuse along the dorsal midline of the tube, whereas the proximal and distal edges of these enlarged basal scales meet and sometimes fuse with those of adjacent whorls, altogether forming a somewhat porous tube that is open at both ends. Occasionally, small coenenchymal scales that project perpendicular to the branch will fill in the spaces between basal scales of adjacent whorls. Although an obvious advantage is gained for the worm in this association, no advantage can be conjectured for the gorgonian.

Several specimens, collected at the margins of the known distribution, show some variation in morphology. The single specimen known from the northern Gulf of Mexico (USNM 89124) has a very low operculum, like that of *C. johnsoni*, but otherwise is similar to *C. imbricata*. The colonies from Bermuda (USNM 75104) and San Pablo Seamount (USNM 57552) have unusually large polyps, 4.0 and 3.2 mm, respectively, but are otherwise similar to *C*. *imbricata*.

Acknowledgments

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Associate Editor: Stephen L. Gardiner

APPENDIX: Station Data

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Date
		U.S.F.C.S Albatr	oss	
2342	23°10'39"	82°20'21"	384	19 Jan 1885
2343	23°11'35"	82°19'25"	510	19 Jan 1885
2346	23°10′39″	82°20'21"	366	20 Jan 1885
2354	20°59'30"	86°23'45"	238	22 Jan 1885
2416	31°26′	79°07′	505	1 Apr 1885
2662	29°24'30"	79°43′	794	4 May 1886
2663	29°39′	79°49′	770	4 May 1886
2666	29°47′30″	79°49′	494	5 May 1886
2667	30°53'	79°42′30″	499	5 May 1886
2668	30°58'30"	79°38'30"	538	5 May 1886
2669	31°09′	79°33'30"	644	5 May 1886
2753	13°34′	61°03′	514	4 Dec 1885
1119-19	off Beaufor	N Carolina	2	27 May 1949
	on beautor	Aluin (cubmarcib		27 may 1919
77-760	27°04 9'	79°20.1'	613-654	Jun 1977
77-761	27°04′	70°18.8'	600	Jun 1977
77.762	27'03 3'	70°20.0'	600	Jun 1977
77 764	27 05.5	79 20.0	410	Jun 1977
016	21 33.0	79 09	410	2 Nov 1079
840 1225	20 20	77.32	525	3 NOV 1978
1333	27 03	(2)22.0/	1000	21 Feb 1984
3883-3	33 40.17	62 33.9	1821	4 Jun 2003
3903-101-2	38'47.33'	64°07.95'	2063	15 Jul 2003
		Anton Dohrn		
6392	30°49′	79°49′	400	?
65-32	Tor	tugas	1064	30 Jul 1932
		NV Ananns (A	(1)	
266-02	31°58′	77°18.5′	813	25 Jun 1961
266-04	31°56′	77°26′	768	26 Jun 1961
266-07	31°53′	77°23′	750	28 Jun 1961
266-40	30°53′	78°47′	804	13 Jul 1961
266-41	30°59′	78°14′	877	15 Jul 1961
266-47	30°53′	78°47′	819	19 Jul 1961
280-09	38°51′18″	60°29'00"	1902	17 Jun 1962
2999	23°10′	81°29′	265512	17 Mar 1938
3303	23°05′	82°33′	476	23 Mar 1939
3402	22°36′	78°21′	421	28 Apr 1939
3403	22°36′	78°22	384	28 Apr 1939
3438	23°05′	79°37′	485	2 May 1939
3463	23°09′	81°26′	421	9 May 1939
3465	23°09′	81°27′	320	9 May 1939
3466	23°09'	81°27′	366	9 May 1939
3478	23°09′	81°27'30"	240	11 May 1939
3479	23°10′	81°26′	384	11 May 1939
3480	23°10′	81°28′	366	11 May 1939
3482	23°09'	81°27′	348	11 May 1939
3780	30°27′	79°52′	458-485	24 Feb 1940
3782	30°10′	78°44′	795-804	24 Feb 1940
		U. S. C. S. S. B	bb	
19	23°03′	83°10'30"	567	4 May 1868
22	24°14′20″	80°59'40″	567	4 May 1868
135	24°20'30"	81°58'30"	229	17 Feb 1869

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Date
	Johnso	n-Smithsonian Deep-Sea	a Expedition (JS)	
43	18°04′	67°48′	439-549	11 Feb 1933
102	18°51′	64°33'	90-500	4 Mar 1933
103	18°51′	64°33'	274-732	4 Mar 1933
		R/V Cape Flori	da	
v	27021/	70°15′	350 400	In1 1084
^	27 51	7915	550-400	Jul 1984
		R/V Cape Hatte	ras	
SA6	31°18′08″	79°00'08″	545-549	17 Nov 1985
SA6-1	31°17′18″	79°00′39″	572-575	17 Nov 1985
SA6-5	31°49′40″	78°19′16″	625	18 Nov 1985
		R/V Colombus Iseli	n (CI)	
63	28°06′	77°08′	1023-1153	21 Sep 1980
123	24°12′06″	77°18′	1435	24 Sep 1973
140	26°24′	79°36′	738	28 Sep 1973
246	26°23′	79°37′	743-761	29 Oct 1974
266	24°18.5′	77°11.7′	?	3 Nov 1974
	*	Clelia (submersit	ole)	
78	32°43′38″	78°05'38″	175-196	5 Jul 1993
79A	32°43′38″	79°05′50″	210	7 Jul 1993
		M/V Combat		
174	34°45′	75°28'	320	14 Nov 1956
368	34°15′	75°23'	348	16 Jun 1957
500	5115	Discourses	540	10 341 1937
v	32°10/	79%07/19	446	5 Oct 1067
^	52 10	780718	440	5 001 1907
		K/V Eastwara		
26004	28°08′	79°33′	785830	Nov 1974
26017	26°38′30″	79°32′30″	775	Nov 1974
26019	27°16′48″	79°25′	655-685	Nov 1974
26022	27"28'30"	79°25′18″	655-685	Nov 1974
26023	27'32'	79°22′	690	Nov 1974
26028	27°09.5′	79°25′	635-700	Nov 1974
26031	27°00′	79°24′18″	645-690	Nov 1974
26052	25°42.7'	79°47.5′	660-770	Nov 1974
26535	27°17.6′	79°15.6′	480	29 Mar 1975
26537	27°14′	79°15′	520	29 Mar 1975
26538	27°12′	79°13.7′	420	29 Mar 1975
26547	27°18′	79°17′	520	Mar 1975
26549	27°17′30″	79°12′30″	370	30 Mar 1975
26550	27°16′24″	79°14′18″	440	30 Mar 1975
26559	26°30.3′	79°14.7′	?	31 Mar 1975
31281	26°53′54″	79°07′18″	320	1977
		R/V Gerda (G)	
56	25°31′	79°20′	458	28 Aug 1962
169	27°01′	79°21.5′	229-275	29 Jun 1963
170	27°06'	79°32′	659-677	29 Jun 1963
177	27°17′	79°34′	686	30 Jun 1963
235	25°44'	79°22′	531	30 Jun 1963

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Date
241	25°26′	79°18′	494-502	30 Jan 1964
242	25°36'	79°21′	485-530	30 Jan 1964
246	26°57'	79°12.5′	512	5 Feb 1964
247	27°07′	79°21′	567	5 Feb 1964
251	27°25′	78°41′	293-311	5 Feb 1964
252	27°29.5'	78°37.5′	485-496	5 Feb 1964
254	27°34.5′	78°49′	488-516	6 Feb 1964
261	27°20′	79°22′	494-511	7 Feb 1964
386	27°09′	78°18′	604	19 Sep 1964
387	27°17′	79°15′	412	19 Sep 1964
391	27°20′	79°12′	?	19 Sep 1964
533	26°27′	78°43′	383-403	4 Mar 1965
598	24°47′	80°26′	183	15 Apr 1965
633	25°59′	79°19′	479-458	30 Jun 1965
647	26°16′	79°43′	520-549	15 Jul 1965
660	26°59′	79°21′	631	17 Jul 1965
661	27°07′	79°32′	695-718	17 Jul 1965
664	27°35′	79°22'	567	17 Jul 1965
672	27°53′	79°03′	796	18 Jul 1965
679	25°56′	78°09′	595-711	20 Jul 1965
680	25°56′	78°05′	571-657	20 Jul 1965
692	26°34'	78°25′	329-421	21 Jul 1965
695	26°28′	78°37′	535-575	22 Jul 1965
696	26°28'	78°43′	458-467	22 Jul 1965
704	26°20'	78°40′	275-366	22 Jul 1965
706	26°27′	78°43′	489-522	22 Jul 1965
707	26°27'	78°40′	514-586	22 Jul 1965
785	24°30'	80°40′	205-210	16 Aug 1966
808	24 35	70°33′	751	13 Sep 1966
835	20 30 24°22'	81°11′	187_198	11 Jul 1967
859	23°54'	81°57′	1160-1190	21 Aug 1967
870	21.00	86°25′	210	9 Sep 1967
880	20%55/	86°28'	175-220	10 Sep 1967
807	20°50'	86°24'	210-290	10 Sep 1967
898	21°04′	86°19'	340-360	10 Sep 1967
800	20°57/	86°34′	40-164	10 Sep 1967
936	26°35′	79°20'	600	1 Oct 1967
965	23%45/	81º40'	1394-1399	1 Ech 1968
1012	23°35'	70°33′	509-531	14 Jun 1968
1125	25 55	70%05/	900-950	17 Jun 1968
1312	26°38′	79°02′	505-527	31 Mar 1971
1314	26'52'	70°11′	532	2
1514	20.52	R/V Gosnold ((Cor)	·
2244	209201	77900 5/	000	9
2344	30 29	77 29.5	882	27 4 10/5
2383	30'56'24'	78'34'18'	809	27 Aug 1965
2304	30 34 24	78 44 00	820	27 Aug 1965
2303	30 57 12	78'54'30	579	27 Aug 1905
2367	31 14 48	78 59 00	530	27 Aug 1965
2413	30'14.5	79'44.7	383-022	2 Sep 1905
2414	20010	79 35.1	494	5 Sep 1965
2401	28 14.4	79'30.5'	850	15 Sep 1905
2409	29 43 12	79.51.48	040	10 Sep 1905

APPENDIX: Continued

APPENDIX: Continued

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Date
	м	/V, R/V Oregon and O	regon II (O)	
1328	24°33'	83°34′	366	Jul 1955
1343	22°59′	79°17′	457	Jul 1955
1349	24°03′	80°30'	274	18 Jul 1955
4940	20°30'	86°14′	310-330	12 Jun 1964
11703	30°28′	79°51′	494	19 Jan 1972
11705	30°26′	79°44′	640	19 Jan 1972
11716	30°52′	79°39′	576	21 Jan 1972
11717	30°52'	79°34′	658	21 Jan 1972
11725	31°44′	79°02′	543	22 Jan 1972
11726	31°42′	78°53′	512	12 Jan 1972
		R/V Gyre		
CO4	27°28'06"	89°43′36″	1358-1518	13 Apr 1984
		R/V Pillsbury ((P)	
105	30°28′	79°42′	388-403	27 Jul 1964
197	27°59′	79°20′	567-586	11 Aug 1964
209	26°59′	79°16′	550	12 Aug 1964
592	21°00′	86°23′	180	15 Mar 1968
594	21°00.5'	86°23.0'	330	15 May 1968
596	24°42′	80°32′	137	15 May 1968
598	21°07′	86°21′	155-205	15 May 1968
881	13°20.8'	61°02.5'	576-823	6 Jul 1969
892	14°17′	60°45'12"	1236-1313	6 Jul 1969
954	16°55′	62°43′	686-1125	16 Jul 1969
1146	20°08′	73°27′	1110-1189	14 Jun 1970
		M/V, R/V Silver Bo	ay (SB)	
440	27°21′	79°15′	439-503	8 Jun 1958
453	29°38′	78°26′	879	12 Jun 1958
5190	18°24′	68°05′	366	17 Oct 1963